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Heritability and genetic correlations between rumination time and production traits in Holstein dairy cows during different lactation phases

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Abstract

So far, rumination has been used as a proxy for monitoring dairy cow health at farm level. However, investigating its genetic aspects as well as its correlation with other important productive traits may turn this management tool into a new informative selection criterion. However, scientific evidences on genetic correlation among rumination time (RT) and milk production and milk composition are still scarce. Therefore, the objective of this study was to estimate the heritability of RT across three lactation phases and its genetic correlation with milk production, milk composition and somatic cell count (SCC). Results of our study showed that heritability for RT was 0.34 and was constant across lactation. The mean genetic correlations between RT and milk production and composition traits were 0.07 (milk production), -0.07 (protein yield), -0.31 (fat yield), and -0.32 (fat/protein ratio). The mean genetic correlation between RT and the SCC was 0.05.

KEYWORDS

dairy cow, gibbs sampling, heritability, rumination time

1 | INTRODUCTION

Rumination is the process of regurgitation, remastication, salivation and swallowing of ingesta (Erina et al., 2013) and is a key physiological function that provides the effective mechanical breakdown of roughage and thereby increases the substrate surface area to fermentative microbes. The microbial community is composed by bacteria, protozoa and fungi that, by fermentation, produce substances that are then absorbed into the rumen by the cow. This production supplies about 60%–80% of the cow's energy. Different species of bacteria and protozoa have different roles (e.g., some digest cellulose while others digest starch and sugar). The end products of microbial fermentation are volatile fatty acids, ammonia and proteins (Moran, 2005). The rumination process is influenced by the fibre

content in the feed, especially by the neutral-detergent fibre fraction that is mainly composed by cellulose and lignin (Dado & Allen, 1995). Differently from the past, when rumination was visually monitored by researchers, today rumination time (RT) is often measured by automatic recording systems that monitor the welfare status of the dairy cows, that are nowadays often present in large commercial farms (Borchers & Bewley, 2015). The recording systems store information every minute and then summarize this data on an hourly basis. Thus, there is a large amount of interesting information that could be used as new proxies in dairy cattle breeding strategies.

Although rumination activity has been studied thoroughly from both the physiological and the pathological point of view, its genetic component is still almost completely uninvestigated. Ideally, to be a valuable selection criterion, RT should have a moderate-to-high heritability and should be genetically correlated with other important traits. Only recently, Moretti et al. (2016) and Byskov, Fogh, and Løvendahl (2017) published a first estimate of RT heritability in Italian and Danish Holstein dairy cows, respectively. In both estimates, RT heritability was 0.32, a value usually considered as moderate. Moreover, Byskov et al. (2017) estimated the genetic correlation between RT and feed-related variables. Their results showed that RT was negatively correlated with dry matter intake and residual feed intake. Other meaningful parameters in dairy cow selection systems are the ones related to milk production and composition. Important selection traits in cattle such as milk yield (MY), protein (PY) and fat (FY) yield and somatic cell count (SCC) have been studied thoroughly, and their heritabilities have been evaluated in several herds, breeds and environments (e.g., Hoekstra, van der Lugt, van der Werf, & Ouweltjes, 1994; Suzuki & van Vleck, 1994). In a review covering a 100-year window of Holstein genetic selection history, Miglior et al. (2017) summarized the heritability values for the main traits used in cattle breeding. According to this review. MY heritability ranged from 0.20 to 0.55, PY ranged from 0.17 to 0.50, and FY from 0.15 to 0.57. SCC heritability ranged from 0.05 to 0.35.

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As of today, the genetic correlation between milk production parameters and RT has not been evaluated, with the exception of the genetic correlation with energy-corrected milk, evaluated by Byskov et al., 2017. Thus, the aim of the study was to investigate the genetic variation and to estimate the heritability of RT and its genetic correlation with MY, PY, FY and SCC. If RT is going to be used a proxy for feed efficiency and/or animal welfare, its genetic relationship with other economical important traits must be estimated. Furthermore, following the above-mentioned results, the question about the possibility to use RT as a welfare proxy was addressed.

2 | MATERIALS AND METHODS

2.1 | Data

The Heatime HR system (SCR Engineers Ltd., Netanya, Israel) automatic recording system was used in this study. This system is composed of a neck collar with a tag placed on the left side of the neck, containing a microphone to monitor rumination and a three-axis accelerometer to quantify neck activity. Third-party validation on this technology was performed (Burfeind et al., 2011; Schirmann, von Keyserlingk, Weary, Veira, & Heuwieser, 2009), which confirmed the monitoring accuracy of the recorded variables. Other information regarding the animal (e.g., ID number, age, parity) was collected from the annexed herd management software. Records for 710 Holstein dairy cows were available, coming from four different private farms, all located in the Po Valley in Northern Italy. Each farm managed the feeding independently, with different formulation of total mixed ration. For each cow, information about sire, dam, parity and age at last calving was collected from the herd management software, while daily RT, daily MY and days in milk (DIM) were retrieved from the automatic recording system. The available records ranged from September 2014 to May 2017. On average, 473 daily observation was available for each cow in the data set.

Daily production traits, comprising FY, PY and SCC, were recorded monthly by the Italian Breeder's Association and adhered to the International Committee for Animal Recording (ICAR) standards (International Committee for Animal Recording, 2017). SCC data were normalized as follows:

$$\text{LogSCC} = \log_2 \frac{\text{SCC}}{100} + 3.$$

Contemporary groups were defined by merging herd, year and month of the test-day. Contemporary groups with less than five animals were deleted.

To evaluate RT at different DIM, each lactation was divided into three phases, namely an early phase (0-60 DIM), a mid phase (61-150 DIM) and a late phase (151-300 DIM). Each daily record was then assigned to a different phase according to its DIM. To obtain a single value for each trait (i.e., each lactation phase), all the observations per animal clustered in the same phase were averaged. Using this approach, RT in the various phases could be treated as different traits and a multivariate analysis was used to investigate its genetic trend at different lactation phases (Mrode, 2013). To make sure that every cow had the whole set of 2-hr intervals recording of RT, data were inspected and edited when needed. Uncomplete sets were accordingly removed. The recording system has proved to be reliable, and the number of removed data was not significantly affecting the number of total observations. Data editing and descriptive statistics were performed using R (version 3.2.5; R Foundation for Statistical Computing, Vienna, Austria). The choice of not using a different approach for modelling individual test-day records (e.g., Random Regression) was mainly related to the size of the data set. When using a Random Regression or a Covariance Function, the goodness of fit depends on the polynomial order of fit, that is the number of parameters to be estimated per animal (Pool & Meuwissen, 2000). When few information are available, the number of parameters has to be reduced and eventually the estimated variance across lactation might increase. For this reason, we decided to use a more conservative and simplified approach, that is a multitrait approach.

2.2 | Statistical models

The (co)variance and breeding values were estimated by both restricted maximum likelihood (REML) using the BLUPF90 software (Misztal, 2012) and by bi- and tricharacteristic Bayesian models using the Gibbs sampler of the GIBBSF90 software (Misztal, 2012). The models used in this study included both an additive genetic and a permanent effect as random effects and the age at last calving, DIM, the parity and the effect of contemporary groups as fixed effects. RT, MY, PY, FY, FY/PY and LogSCC were the traits to be evaluated. The matrix model used for RT was:

$$y = X\beta + Za + e$$

where y = vector of observations of the dependent variable (rumination); $\beta =$ vector of contemporary group, associated with y through the incidence matrix of X; a = vector of random effects of additive genetic value of the animal associating a with y through the incidence matrix Z; and e = vector of residual effects.

For the Bayesian analysis, the effects included in the model were considered to be random variables. For the values of the a priori distribution of variances, values based on bibliographic references for the Holstein breed were assumed.

Initially, for all traits, a single chain of 400,000 iterations was used, with a period of disposal (i.e., "burn-in") of 40,000 iterations, and a sampling interval (i.e., "thinning") of 10. However, these values in some cases have been altered according to the need to adjust for convergence (Raftery & Lewis, 1992). The convergence of the Gibbs chain was therefore tested by the criterion of Geweke. The convergence of the algorithm was verified with a significance level of 0.05 for the test, under the null hypothesis. In this case, the test considers the null hypothesis to be the convergence of the chain; therefore, the larger the *p*-value (> 0.05), the greater is the convergence of the chain (Geweke, 1992). The Bayesian Output Analysis (BOA version 1.1.5) package (Smith, 2005) was used to calculate the mean and the SD for all parameters from the individual marginal posteriors.

The coefficient of direct heritability for all variables was estimated by:

$$h^2 = \sigma_A^2 / \sigma_P^2$$

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3 | RESULTS

Descriptive statistics of the variables and analysed traits are presented in Table 1. The results of the analysis of variance confirmed that there was a statistically significantly difference between the analysed traits in the different lactation 295

TABLE 1 Descriptive statistics (mean \pm *SD*) of the variable available in the data sets, divided into early (0–60 days, 1,605 observations), mid (61–150 days, 1,116 observations) and late (151–300 days, 1,045 observations) lactation phases

	Phases						
Variables	Early	Mid	Late				
Parity	$2.1^{a} \pm 1.2$	$2.0^{a} \pm 1.2$	$1.9^{b} \pm 1.1$				
Age at calving (months)	$40.2^{a} \pm 17.5$	$44.4^{\rm b} \pm 21.5$	$48.5^{\circ} \pm 24.2$				
DIM	$32.7^{\rm a} \pm 9.9$	$103.9^{\rm b} \pm 13.5$	$250.4^{\circ} \pm 59.7$				
RT (minutes/ day)	$512.9^{a} \pm 109.5$	$508.9^{a} \pm 101.4$	$487.3^{\text{b}} \pm 108.9$				
MY	$37.4^{\rm a} \pm 10.2$	$38.5^{\rm b} \pm 8.4$	$30.8^{\circ} \pm 6.9$				
РҮ	$3.1^{a} \pm 0.3$	$3.2^{b} \pm 0.3$	$3.5^{c} \pm 0.3$				
FY	$4.0^{\rm a} \pm 1.0$	$3.8^{b} \pm 0.6$	$4.0^{\rm a} \pm 0.6$				
FY/PY	$1.3^{\rm a} \pm 0.3$	$1.2^{b} \pm 0.2$	$1.1^{c} \pm 0.1$				
LogSCC	$237.9^{a} \pm 647.1$	$226.0^{\rm b} \pm 465.1$	$268.6^{\circ} \pm 458.9$				

a,b Values within a row with different superscripts differ significantly at p < 0.05.

DIM: days in milk; FY/PY: fat and protein yields ratio; FY: fat yield; LogSCC: somatic cell count on a logarithmic base; MY: milk yield; PY: protein yield; RT: rumination time.

phases. Specifically, a *t*-test confirmed that RT was higher (p < 0.05) during early and mid lactation phases and decreased in late phase. Regarding the analysed traits, MY was different between lactation phases (p < 0.05) and showed the higher value during the mid phase. PY showed statistically difference as well (p < 0.05), increasing through the phases. FY in early and late phases was not significantly different (p = 0.1). The FY/PY ratio decreased through the lactation phases (p < 0.05). Lastly, the LogSCC was significantly different (p < 0.05) through all the phases, with the highest value during the late phase.

The phenotypic correlations between RT and milk production parameters were generally low, and ranged from -0.142 (RT vs MY, late lactation phase) to 0.094 (RT vs LogSCC, late lactation phase) (Table 2). In the early phase, all the correlations were not significantly different from 0.

The heritability of RT was estimated using both REML and Bayesian approaches. The two approaches gave similar results. Gibbs sampling method results (Bayesian approach) are reported here (Table 3). In detail, the heritability was estimated to be 0.32 in the early, 0.34 in the mid, and 0.35 in late lactation phase. This results confirmed the previously heritability values estimated by Byskov et al. (2017).

The genetic correlations between RT and milk production parameters were moderate-to-low, ranging from -0.40(RT vs FY/PY ratio, early lactation phase) to 0.13 (RT vs MY, mid lactation phase). Specifically, the genetic correlation between RT and MY during the early phase was slightly negative (-0.04), while being positive in both the WILEY Animal Breeding and Genetics

TABLE 2 Phenotypic correlations for rumination time (RT) vs milk yield (MY), protein yield (PY), fat yield (FY), fat/protein (FY/ PY) ratio and Log somatic cell count (LogSCC) in the three lactation phases (namely, early: 0–60 days; mid: 61–150 days; and late: 151–300 days)

Parameter	Phase	Phenotypic correlation	Posterior standard deviation	Significance ^a
RT vs MY	Early	-0.005	0.032	ns
	Mid	-0.089	0.034	**
	Late	-0.142	0.035	***
RT vs PY	Early	-0.058	0.061	ns
	Mid	-0.069	0.062	*
	Late	-0.090	0.064	**
RT vs FY	Early	-0.004	0.035	ns
	Mid	-0.124	0.034	***
	Late	-0.095	0.037	**
RT vs FY/ PY	Early	0.016	0.034	ns
	Mid	-0.094	0.034	**
	Late	-0.045	0.035	ns
RT vs LogSCC	Early	0.023	0.037	ns
	Mid	0.041	0.033	ns
	Late	0.094	0.035	**

^aThe significance codes are: 0 < *** < 0.001 < ** < 0.01 < * < 0.05 < ns.

mid and the late phases (0.13 and 0.12, respectively). The genetic correlation with PY and FY was negative for all the lactation phases (0.00, -0.05, and -0.17 in PY, and -0.39, -0.22, and -0.33 in FY for early, mid and late phases respectively), and, straightforwardly, the genetic correlation between RT and FY/PY ratio was similarly negative (-0.40, -0.23, and -0.32 for early, mid and late phases, respectively). The genetic correlation with LogSCC ranged from -0.10 (late lactation phase) to 0.30 (early lactation phase), with a value of -0.05 for the mid phase.

The variability in estimated heritability values for milk production parameters was higher than the variability in estimated heritability value for RT. MY heritability increased through the lactation phases, with estimated values of 0.14, 0.39, and 0.53 for early, mid and late lactation, respectively. The same increasing trend was shown by the heritability estimates for PY (mean value of 0.53, with 0.25, 0.50 and 0.83 for early, mid and late lactation, respectively), FY (mean value of 0.44, with 0.18, 0.46, and 0.68 for early, mid and late lactation, respectively), and FY/PY ratio (mean value of 0.32, with 0.14, 0.33, and 0.50 for early, mid and late lactation, respectively). Lastly, LogSCC heritability, on average, was 0.23, with a similar heritability in early and late phases (0.25 and 0.26, respectively) and a lower one (0.19) in mid phase.

4 | **DISCUSSION**

The descriptive statistics (Table 1) did not show any abnormal behaviour regarding variables and traits. It could be hypothesized that the highest value of RT in the initial phase compared to the others is due to the higher feed consumption by the animal. This increase in feed consumption is needed by the cow to meet the high-energy requirements during the initial lactation phase. Indeed, at the beginning of lactation, the MY, the milk proteins, fat and lactose increase rapidly, exceeding feed intake (Bertoni, Trevisi, & Lombardelli, 2009).

Monitoring of RT, mainly during the first week of lactation, has been used as a mean of timely identification of cows at high risk of disease development during early lactation (Calamari et al., 2014), probably because in animals affected by diseases RT may decrease because of the reduction in feed intake. The potential use of RT as an indicator of health disorders has also been reported by other authors (Krause & Oetzel, 2006; Liboreiro et al., 2015; Stangaferro, Wijma, Caixeta, Al-Abri, & Giordano, 2016a,b,c).

Milk yield reached its highest value during the mid lactation phase. This trend is typical for a lactation curve, and this knowledge is valuable in management context, especially for time-dependent decisions such as feeding strategies to maintain maximum yields for as long as possible (López et al., 2015).

Laevens et al. (1997) showed that in bacteriologically negative cows, the SCC is not affected by the lactation stage. However, they found a significant effect of lactation phase when bacteriologically positive cows were involved. This second result, which was obtained in similar conditions, is in agreement with our results.

The heritability estimated for RT in our population was similar to the one estimated by Byskov et al. (2017) in a population of Danish Holstein cows. The averaged heritability value found in this study (0.34) is considered a moderate value for heritability, meaning that it could be possible to use this trait in animal selection. Furthermore, our results indicated that the heritability of RT is nearly constant during the whole lactation, with a difference of 0.03 points between the early and the late phases. This result further confirms the possibility to use this trait in a selection strategy.

The average genetic correlation between RT and MY during the entire lactation was close to zero (0.07), implicating that the two traits have an almost null genetic association. The MY heritability value estimated in this study changed heavily during the lactation phases, with the highest value during the late phase. This means that milk production in a late lactation phase is a heritable trait. Selecting for this trait would be advantageous for dairy

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TABLE 3 Heritability (h^2 , mean \pm SD), genetic correlation (r), and Posterior Standard Deviation (PSD) for rumination time (RT) vs milk yield (MY), protein yield (PY), fat yield (FY), fat/protein (FY/PY) ratio and Log somatic cell count (LogSCC) in the three lactation phases (namely, early: 0–60 days; mid: 61–150 days; and late: 151–300 days). For each couple of traits, additive (σ_a^2) and residual (σ_e^2) variances are reported

		Rumination time			Second trait				
Parameter	Phase	σ_a^2	σ_e^2	h^2	σ_a^2	σ_e^2	h^2	r	PSD
RT vs MY	Early	$2,399.4 \pm 425.9$	$5,164.8 \pm 358.3$	0.32 ± 0.05	8.35 ± 2.79	51.57 ± 3.20	0.14 ± 0.04	-0.04	0.19
	Mid	$2,543.9 \pm 414.2$	$4,967.6 \pm 330.8$	0.34 ± 0.05	15.70 ± 2.39	24.84 ± 1.73	0.39 ± 0.05	0.13	0.10
	Late	$2,830.7 \pm 487.7$	$5,442.0 \pm 386.7$	0.34 ± 0.05	14.91 ± 1.70	13.52 ± 0.99	0.53 ± 0.04	0.12	0.10
RT vs PY	Early	$2,437.4 \pm 412.9$	$5,154.7 \pm 352.1$	0.32 ± 0.05	0.02 ± 0.00	0.06 ± 0.00	0.25 ± 0.04	0.00	0.15
	Mid	$2,504.6 \pm 419.6$	4,998.9 ± 338.9	0.33 ± 0.05	0.02 ± 0.00	0.02 ± 0.00	0.50 ± 0.04	-0.05	0.10
	Late	$2,961.8 \pm 493.4$	5,379.9 ± 377.4	0.36 ± 0.05	0.05 ± 0.00	0.01 ± 0.00	0.83 ± 0.02	-0.17	0.09
RT vs FY	Early	$2,437.4 \pm 412.9$	$5,154.7 \pm 352.1$	0.32 ± 0.05	0.10 ± 0.03	0.46 ± 0.03	0.18 ± 0.04	-0.39	0.16
	Mid	2,504.6 ± 419.6	4,998.9 ± 338.9	0.33 ± 0.05	0.16 ± 0.02	0.19 ± 0.01	0.46 ± 0.04	-0.22	0.10
	Late	$2,961.8 \pm 493.4$	5,379.9 ± 377.4	0.36 ± 0.05	0.21 ± 0.02	0.10 ± 0.01	0.68 ± 0.03	-0.33	0.08
RT vs FY/PY I ratio I	Early	$2,465.1 \pm 420.5$	$5,127.9 \pm 350.4$	0.33 ± 0.04	0.01 ± 0.00	0.06 ± 0.00	0.14 ± 0.04	-0.40	0.18
	Mid	$2,556.4 \pm 417.0$	4,958.9 ± 329.4	0.34 ± 0.05	0.01 ± 0.00	0.02 ± 0.00	0.33 ± 0.04	-0.23	0.11
	Late	$2,949.4 \pm 509.0$	5,378.8 ± 385.9	0.35 ± 0.0	0.01 ± 0.00	0.01 ± 0.00	0.50 ± 0.04	-0.32	0.09
RT vs LogSCC	Early	$2,372.6 \pm 425.9$	$5,183.7 \pm 358.5$	0.31 ± 0.05	0.85 ± 0.18	2.62 ± 0.17	0.25 ± 0.05	0.30	0.16
	Mid	$2,525.9 \pm 417.8$	4,973.4 ± 336.4	0.34 ± 0.05	0.58 ± 0.14	2.51 ± 0.15	0.19 ± 0.05	-0.05	0.14
	Late	$2,863.3 \pm 486.0$	5,423.2 ± 379.7	0.35 ± 0.05	0.58 ± 0.11	1.67 ± 0.11	0.26 ± 0.04	-0.10	0.13

farms. The average value through the lactation was 0.35, similar to the values obtained in other Holstein herds in Europe (Miglior et al., 2017). These results confirm the possibility to select animals to improve MY. As the heritability of this trait is moderate, the selection of bulls, even considering the first lactation production information only (Filho, Verneque, Torres, Ribeiro, & Toral, 2015), can be an efficient tool to modify the average of this trait over generations.

Fat yield genetic correlation with RT was negative as well, but it was higher in absolute value (-0.31). Estimated heritability for FY was 0.44, higher than what reported for some other Holstein populations (e.g., 0.30 in Japanese Holstein, Suzuki & van Vleck, 1994; 0.36 in Dutch Holstein, Hoekstra et al., 1994), but remaining in the range described by Miglior et al. (2017). The selection for RT would probably results in animals with a more stable daily RT. These animals would probably better cope with situations in which RT typically decreases. However, this correlation is economically unfavourable because of an increase in daily RT would lead to a decrease in FY in milk. Furthermore, milk fatty acids are of specific importance in human nutrition (Chilliard et al., 2007), as well as their contribution to the sensorial quality of milk products and to the energy supply they provide (Parodi, 2004). According to Toral et al. (2015), milk fat synthesis represents a significant energy cost for milk production and plays a central role in determining the quality of dairy products and the partitioning of energy in milk.

The average genetic correlation between RT and PY was -0.11, indicating a weak negative genetic association. Estimated heritability for PY in our population was 0.53, much higher than what is reported in the literature (0.26 in)Japanese Holstein, Suzuki & van Vleck, 1994; 0;.33 in Dutch Holstein, Hoekstra et al., 1994). Regarding the FY/ PY ratio, which is used as an indicator for subclinical ketosis diagnosis (Jenkins et al., 2015), its correlation with RT was -0.32, and its heritability was 0.32. Given this negative association, selection for higher daily RT would have negative effects on this ratio. It is thus important to properly define the selection goal using RT because of fat/protein ratio of milk could be affected by this decision. These components are probably two of the most important economic traits for dairy milk production. Feed management is probably the simplest and quickest way to control FY/PY ratio (de Quadros & Lobato, 1997).

Lastly, the heritability of LogSCC was 0.23, similar to what reported in Holstein (Miglior et al., 2017). LogSCC average genetic correlation with RT was small (0.05), although it was higher during the early phase of lactation (0.30). It is hypothesized that at this stage, the animal consumes more food and in parallel, the greater presence of LogSCC occurs due to the presence of immunoglobulins and consequently of defence cells. It is presumable to ILEY Animal Breeding and Genetics

hypothesize that the ability to relate RT to mastitis may be influenced by the severity of systemic illness and type of mastitis-causing pathogen; however, the rumination monitoring system is useful for identifying animals with abomasal displacement, ketosis, metritis and mastitis earlier than farm personnel (Stangaferro et al., 2016a,b,c).

5 | CONCLUSIONS

In conclusion, RT was found to have a moderate heritability in Holstein dairy cows reared in Northern Italy, and therefore, could be used in a breeding programme. However, its negative (although weak) genetic correlations with milk production traits, along with the positive association with SCC, showed that daily RT should be used carefully in dairy cows selection. Selection for medium level of RT would be probably the best option to balance the positive effects of RT and the negative effects linked to its genetic correlations.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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